

A REVISION OF *ACASTE DOWNINGIAE* (MURCHISON) AND RELATED TRILOBITES

by J. H. SHERGOLD

ABSTRACT. Three species of *Acaste*, *A. downingiae* (Murchison), *A. inflata* (Salter), and *A. subcaudata* (Murchison); two species of *Acastocephala* gen. nov., *A. macrops* (Salter) and *A. dudleyensis* sp. nov.; and *Acastoides constricta* (Salter) are described from rocks of Wenlockian age from the West Midlands, Welsh Borderlands, and South Wales. Their relationships to later Silurian and early Devonian acastomorph genera are discussed.

THE species *Calymene? downingiae* was first recognized by Murchison (1839) who divided it from *Calymene macrophthalma* Brongniart on account of its smaller eyes and well-developed glabellar furrows. The species was subsequently placed in the genus *Phacops* by Emmerich (1845) and by Salter (1848, 1853), M'Coy (1851), and Murchison (1859). Goldfuss (1843) established the genus *Acaste*, which was regarded as a subgenus of *Phacops* by Salter (1864). *Acaste downingiae* was the first of a group of eight species listed by Goldfuss (1843, p. 563) and has been regarded by subsequent authors as the type species although this was not definitely established until 1959 (Struve in Moore, 1959, p. O488). R. Richter (1909) and R. and E. Richter (1939, 1952, 1954) discussed the morphology, relationships, and successions of acastomorph trilobites but concentrated their attention mainly on Devonian genera.

Salter (1864) divided the species into six varieties which he distinguished by Greek letters. At the present time these are assigned to the following taxa. After the revision of R. and E. Richter (1954, p. 16) var. α , *vulgaris* becomes *Acaste downingiae* (Murchison) s.s. and var. ϵ , *constrictus* is assigned to the genus *Acastoides* Delo 1935, becoming *A. constricta* (Salter). Var. δ , *spinosus* was chosen by Reed in 1925 as the type species of *Acastella*. Two further varieties are revised below. Var. γ , *inflatus* has been retained in the genus *Acaste* as *A. inflata* (Salter). For trilobites previously referred to var. β , *macrops* a new genus, *Acastocephala*, has been erected to include two species, *A. macrops* (Salter), the type species and *A. dudleyensis* sp. nov. Salter's var. ζ , *cuneatus*, based on a poorly preserved cephalon from the Denbigh Grits of Llanrwst, is the only specimen known from that area and until further material becomes available cannot be adequately described.

The present paper is based mainly on materials from the Wenlockian of the West Midlands, Welsh Borderlands, and South Wales in the following collections: the Sedgwick Museum, Cambridge (SM); Oxford University Museum (OUM); Birmingham University Museum (BU); the British Museum (Nat. Hist.) (BM); the Geological Survey Museum (GSM); the Geological Society Collection (GSC); and the National Museum of Wales (NMW). Additional material has been used from the Bristol City Museum; the Ludlow Museum; the Hancock Museum, Newcastle upon Tyne; the Departmental Collections, University of Newcastle upon Tyne (UNT), and from collections made by the author in South Wales.

Relationships of considered genera. Struve (1958b) has used the term 'acastomorphen' for Phacopacea with dalmanitid tendencies as distinct from those with calmonioid tendencies. The writer has here used the term in a somewhat different sense to include

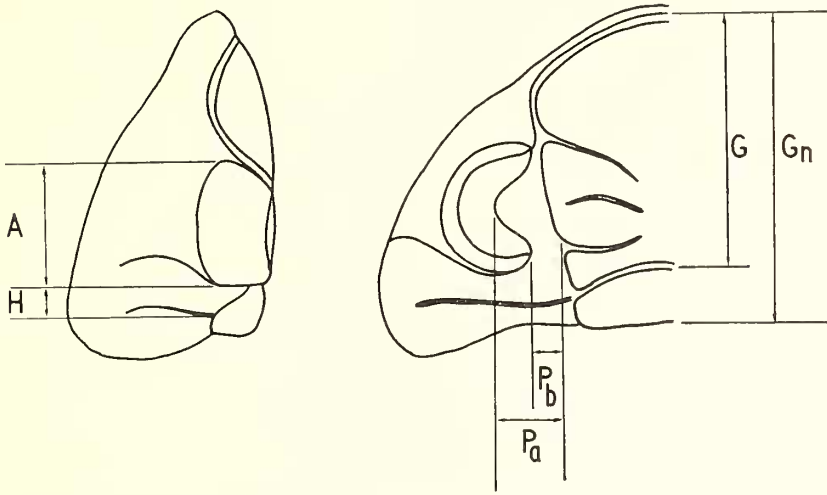
[Palaeontology, Vol. 9, Part 2, 1966, pp. 183-207, pls. 28-32.]

the genera *Acaste*, *Acastoides*, *Acastella*, *Acastellina* R. and E. Richter 1954, *Acastava* R. and E. Richter 1954, and *Acastocephala* gen. nov., feeling that these genera form a closely related Siluro-Devonian complex. In Struve's (1958b, 1959) current classification these genera are grouped into two subfamilies, Acastinae Delo 1935 and Acastavinae Struve 1958. The former is included in the family Calmoniidae and the latter in the Dalmanitidae. The Acastavinae (*Acastava*, *Acastella*, and *Acastellina*) are thought by Struve to show an asteropyginid trend in certain characters, namely the shape of the cephalon, the construction of the genal spines and the poorly segmented pygidium with its marked tendency to develop denticulations along the lateral margins. The Acastinae, while including such genera as *Acaste* and *Acastoides*, embraces also *Scotiella* and *Phacopina*, subgenera in which the glabellar segmentation has become faint or obsolete. The mucronations possessed by members of the Acastinae are thought by Struve to be essentially similar in construction to the Calmoniidae rather than the Dalmanitidae.

During the early holaspid ontogeny of *Acaste downingiae* and *A. subcaudata*, short but distinct genal projections are observed on the posterolateral fixigenal margins. These projections, in effect miniature spines, are rapidly resorbed in succeeding moults. In their construction these spines differ from those produced by the Dalmanitinae and Asteropyginae which are massive continuations of the cephalic margins but are more similar to the small, elegant mucronations shown by such typical calmoniid genera as *Bainella*, *Schizostylus*, and *Paracalmonia* or to those of the acastavinid genus, *Acastella*. In their orientation these small acastid spines contrast with those of the Calmoniidae which are deflected prominently outwards from the line of the cephalic margin, but compare well with those of the Acastavinae, being most closely comparable with the mucronations displayed by the adult of *Acastella prima* Tomczykowa (1962a, pp. 261-2, pl. 1, figs. 2, 4, 5). If the early holaspid mucronations of *Acaste downingiae* were to be continued into the adult stage the condition of *Acastella prima* would be closely approximated (text-fig. 3). The derivation of *Acastella* from *Acaste* through an intermediate form such as *Acastella prima* becomes a strong probability (Tomczykowa 1962b, p. 202).

Acastocephala dudleyensis sp. nov. also possesses small genal mucronations in its early holaspid ontogeny. In the adult condition these are again resorbed and the genae become posterolaterally angled or rounded. The construction and orientation of these spines are essentially similar to the condition shown by the adult of *Acastava atava* (W. E. Schmidt 1907). Further similarities are shown between *Acastocephala* and *Acastava*, for the lateral pygidial margins of young holaspides in both *Acastocephala macrops* and *A. dudleyensis* are provided with three or four pairs of denticulations on the external surface of the shell, similar to those found on the internal mould of the adult *Acastava atava* (text-fig. 5). As with the genal spines, these denticulations are resorbed in the adult which possesses a typically entire margin. Young holaspides, therefore, show the asteropyginid trend of Struve, while the adults with rounded genae and entire pygidial margins do not. In other characters, notably the size and position of the eye and the poorly segmented pygidium, adults of *Acastocephala macrops* are closely comparable to *Acastava atava*. It appears, therefore, that the conditions shown by the early holaspides of *Acastocephala* are retained into the adult stages of *Acastava*. Accordingly *Acastocephala* is thought to be ancestral to *Acastava* and is classified with the Acastavinae.

Two lines of development may thus be postulated among the acastomorph genera. *Acastava* (Siegenian–Emsian) may be derived from *Acastocephala* (Wenlockian) and *Acastella* (Middle Ludlow–?Siegenian) from *Acaste* (Wenlockian–L. Gedinnian). The various Silurian and Devonian species of *Acastoides* (Wenlockian–U. Emsian) appear to be a closely related and distinct group, isolated from other lines of development from Wenlockian times onwards.



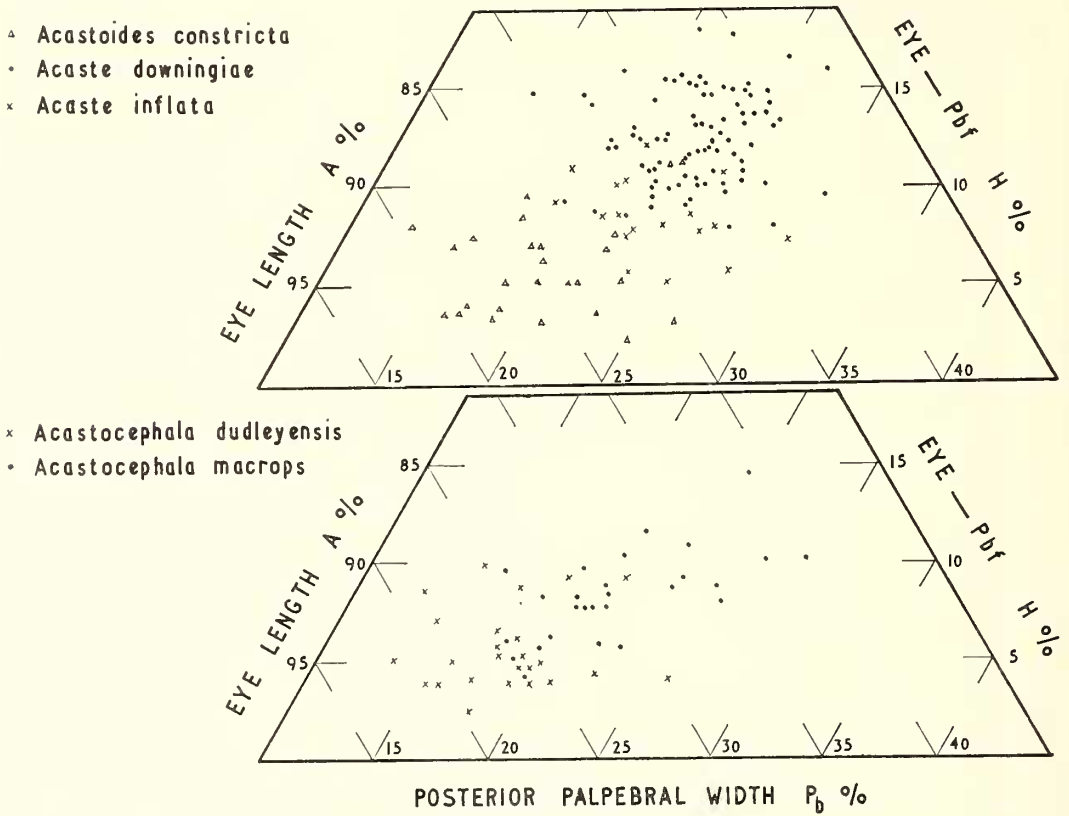
TEXT-FIG. 1. Parameters recorded on a typical acastomorph cephalon.

Measurements. Measurements based on the lengths and widths of the cephalon, thorax and pygidium have been found to be extremely variable and to be largely dependent on preservation. Selected measurements connected with the eye, on the other hand, have shown constancy both intra-generically and intra-specifically. The position of the eye on the cheek with relation to the cephalic margins, posterior border furrow and glabella and the differing relationships between eye length and glabellar length are important in this respect.

The measurements recorded are basically those of Struve (text-fig. 1). They are essentially the eye length, A ; glabellar length, G ; occipital glabellar length, G_n ; and a measurement, H , across the posterior fixigena between the back of the eye and the posterior border furrow. In addition to Struve's parameters, the maximum width, P_a , and the posterior width, P_b , across the palpebral area have been recorded. Of these latter measurements, P_a has been found to depend upon the definition of the palpebral furrow and to be more variable than P_b (see text-fig. 1).

After Struve (1958a), several ratios have been considered important. A/G , the larger eye index; A/G_n , the smaller eye index, and H/A have been used to give some idea of the eye length in relation to glabellar length and the distance of the eye from the posterior border furrow. Values of H/A have shown that in some species the eye remains in a more or less constant position during holaspid ontogeny, while in others it appears to migrate in a posterior direction (see section under *Acastocephala dudleyensis*).

In the text the following glabellar notation is used; preoccipital lobe, 1L; median lateral lobe, 2L; anterior lateral lobe, 3L; 1S, 2S, and 3S are the equivalent glabellar side furrows.



TEXT-FIG. 2. The position of the eye on the cheek plotted with reference to the eye length, posterior border furrow and distance of the eye from the posterior border furrow.

Generic and Specific Differentiation. Characters considered to be of generic importance are as follows: the shapes of both cephalon and pygidium, i.e. the geometry of outline; the segmentation of the pygidium, both in axial and pleural elements; and the size of the eye and its position on the cheek. To illustrate the position of the eye and its relative size the proportionate relationships between A, H, and Pb have been plotted on triangular-based graph paper (text-fig. 2). Further, the development during ontogeny of genal mucronations and pygidial denticulations is of fundamental importance.

Of importance specifically are the convexities (tr. and sag.) of the frontal lobe, 1L and the occipital ring; the height to which the occipital ring is raised above the glabellar side lobes; the shape, in plan view, of the glabella; the number of facets at the maximum height of the visual surface; the convexity (tr.) of the pygidium, both pleural and axial elements; and the width of the pygidial border.

SYSTEMATIC DESCRIPTIONS

Family CALMONIIDAE Delo 1935
 Subfamily ACASTINAE Delo 1935
 Genus ACASTE Goldfuss 1843
Acaste downingiae (Murchison 1839)

Plate 28, figs. 1–18; Plate 29, figs. 1–8

- 1839 *Calymene* ? *Downingiae* (n.s.) Murchison, p. 655, pl. 14, figs. 3a (BU 54) and 3b (specimen untraced).
 1851 *Phacops Downingiae* (Murchison sp.); M'Coy, p. 160 (SM A28766).
 1853 *Phacops Downingiae* Murchison; Salter, pp. 1–12, pl. 1, figs. 1 (BM 44252), 2 (untraced), 4 (GSM 19305), 5–13 (untraced), 15 (untraced).
 1864 *Phacops (Acaste) Downingiae* Murchison, var. α , *vulgaris* Salter, p. 26, pl. 2, figs. 17 (BM 44407), 18 (BU 54), 19–22 (untraced), 23 (BM 44409), 25 (BU 129), also an unnumbered ventral surface between figs. 25 and 34 (BM 44410).
 1864 *Phacops (Acaste) Downingiae* Murchison, var. γ , *inflatus* Salter, p. 27, pl. 2, figs. 31 (GSM 19305) and 33 (GSM 19306).
 1954 *Acaste (Acaste) downingiae* (Murchison 1839); R. and E. Richter, pp. 16–17, pl. 3, figs. 36 (BM In36153), 37–41.
 1965 *Acaste downingiae* (Murchison 1839); Clarkson, p. 11, pls. 1, 2, pl. 3, figs. 1–3.

Lectotype (here designated). Murchison 1839, pl. 14, fig. 3a, BU 54, figured here, pl. 28, fig. 1. Wenlock Limestone, Wren's Nest, Dudley, Worcs.

Diagnosis. A species of *Acaste* with frontal lobe anteriorly depressed and glabellar lobes in general with low convexity (both tr. and sag.). Fixigenae of young holaspides with short, stout mucronate projections which are rapidly resorbed in the succeeding moults to give prominent angulations, these becoming less apparent with further increase in size. Visual surface of eye carrying columns of 8 (rarely 9) lenses alternating with 7 (rarely 8) at the maximum height. Pygidium with 7–9 axial segments, 6–7 pleural segments. In young, pleural field and border area more or less continuous, becoming separated in adult specimens by a shallow furrow or flattening.

Description. Cephalon subtriangular in outline, with narrow, triangular area of librigena projecting in front of the glabella. Surface of test with fine granules. Length of cephalon approximately $\frac{1}{2}$ – $\frac{2}{3}$ width.

Glabella anteriorly rounded, laterally sub-parallel, transverse width decreasing gradually and evenly to posterior; the axial furrows curving very gently round 2L and 3L. Glabella apparently more parallel-sided in large adults than in younger stages. Frontal lobe rounded both anteriorly and antero-laterally, with low to moderate convexity when viewed in lateral profile, large adult specimens having a somewhat greater convexity than immature specimens. 2L and 3L approximately equal in size, with slightly less convexity (trans.) than frontal lobe; abaxially fused. 1L about half as wide (exsag.) as 2L, with little greater convexity (tr.). 3S long, shallow, sigmoidal even in smallest specimens, with a marked posterior median deflection becoming gradually less distinct during ontogeny. 2S shorter than 3S, impressed to a similar depth, transverse or gently curved, with a faint posterior median deflection most pronounced in young forms; failing laterally to reach the axial furrows. 1S wider and deeper than 2S, of similar

length, deflected both medianly and abaxially to the anterior, becoming more transverse, less wide (exsag.) and less deep in later ontogenetic stages. All furrows reaching to within approximately equal distance of the sagittal line. Short median furrow on sagittal line typically present, extending from median extremities of 3S to about one quarter of the length of the frontal lobe.

Occipital furrow abaxially deeper than 1S, becoming shallow but remaining well defined sagittally. Occipital ring narrow (sag.), with slightly less transverse width but greater transverse convexity than 1L; in lateral profile raised slightly above glabellar side lobes at all stages of growth.

Genae gently sloping to a poorly defined border which passes antero-laterally into a narrow (sag.) triangular area of librigena forming the anterior margin of the cephalon. Preglabellar furrow narrow (sag.), shallow. Postocular section of facial suture cutting lateral cephalic margin opposite 1S or mid 2L; preocular section dorsal intramarginal, separating preglabellar furrow from anterior cephalic margin. Fixigenae in smallest holaspides produced postero-laterally into short, stout mucronate projections which in

EXPLANATION OF PLATE 28

Figs. 1–18. *Acaste downingiae* (Murchison 1839). 1, 2. BU 54; figured Murchison 1839, pl. 14, fig. 3a; Salter 1864, pl. 2, fig. 18. Wenlock Limestone, Dudley, Worcs. 1, General view, lectotype arrowed, $\times 1$. 2, Lectotype, cranium, $\times 2$. 3. BU 129; cephalon possibly figured Murchison 1839, pl. 14, fig. 3a (discussed R. and E. Richter 1954, pp. 16–17); Salter 1864, pl. 2, fig. 25. Wenlock Limestone, Dudley, Worcs. Dorsal view of cephalon, $\times 3$. 4–8. BM 44407; figured Salter 1864, pl. 2, fig. 17. Wenlock Limestone, Dudley, Worcs. 4, General view, $\times 1$. 5, Detail, dorsal view of cephalon, $\times 2$. 6, Dorsal view of pygidium and thorax, $\times 2$. 7, Lateral view of cephalon, $\times 2$. 8, Eye showing lens cavities, $\times 8$. 9. BU 129; Eye, $\times 8$. 10–12. GSM 19306; figured Salter 1853, pl. 1, fig. 15 and 1864, pl. 2, fig. 33. Wenlock Limestone, Eastnor, nr. Ledbury, Herefordshire. 10, Lateral view, $\times 3$. 11, Adult pygidium showing border furrow, dorsal view, $\times 3$. 12, View from posterior, $\times 3$. 13–14. GSM 19313; Adult pygidium, Wenlock Limestone, Dudley, Worcs. 13, Dorsal view showing border furrow, $\times 2$. 14, View from posterior, $\times 2$. 15–17. BM 44410; ventral surface figured Salter 1864, pl. 2, no figure number given. Wenlock Limestone, Dudley, Worcs. 15, General view, $\times 2$. 16, Hypostome, $\times 6$. 17, Articulation of posterior five thoracic segments and pygidium (on left), $\times 8$. 18. BM 44252; dorsal exoskeleton, figured Salter 1853, pl. 7, fig. 1. Wenlock Limestone, Dudley, Worcs. $\times 2$.

EXPLANATION OF PLATE 29

Figs. 1–8. *Acaste downingiae* (Murchison 1839). 1. BM 44409; cephalo-thorax figured Salter 1864, pl. 2, fig. 23. Wenlock Limestone, Dudley, Worcs. $\times 2$. 2–3. SM A28717; Wenlock Limestone, Dudley, Worcs. 2, Dorsal view of juvenile pygidium without border furrow, $\times 3$. 3, View from posterior, $\times 3$. 4–6. SM A28744; Wenlock Limestone, Dudley, Worcs. 4, Dorsal view of young holaspide showing genal projection, $\times 4$. 5, Lateral view, $\times 4$. 6, Genal angle, $\times 8$. 7, NMW G.391.2; Wenlock Limestone, Dudley, Worcs. Enlargement of genal angle showing resorption of genal projection, the stage succeeding that of fig. 6, $\times 8$.

Fig. 8. *Acaste? downingiae* (Murchison 1839). GSM 19305; glabella figured Salter 1853, pl. 1, fig. 4, and 1864, pl. 2, fig. 31. Wenlock Limestone, Ledbury, Herefordshire. Dorsal view, $\times 2$.

Figs. 9–16. *Acaste inflata* (Salter 1864). 9–14, OUM C9; Lectotype; figured Salter 1864, pl. 2, fig. 30. Wenlock Limestone, Ledbury, Herefordshire. 9, Dorsal view of cephalon, $\times 3$. 10, Lateral view, $\times 3$. 11, Dorsal view of pygidium, $\times 3$. 12, Posterior view of glabella showing convexities of 2L, 1L, and the occipital ring, $\times 4$. 13, Eye, $\times 8$. 14, Posterior view of pygidium, $\times 3$. 15–16, BM In36154; Wenlock Limestone, Dudley, Worcs. 15, Dorsal view of pygidium, $\times 3$. 16, Posterior view of pygidium, $\times 3$.



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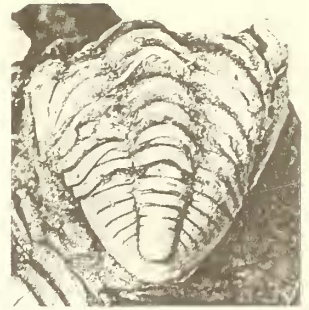
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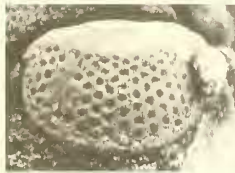
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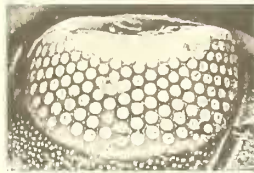
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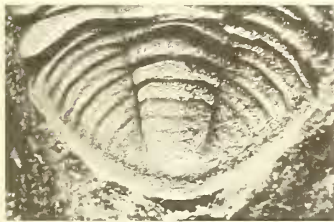
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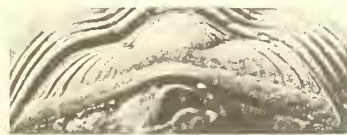
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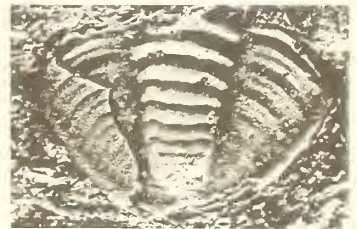
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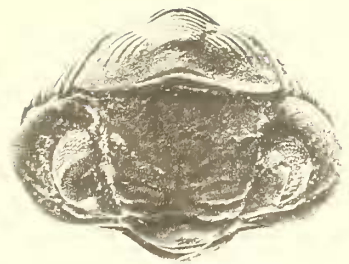
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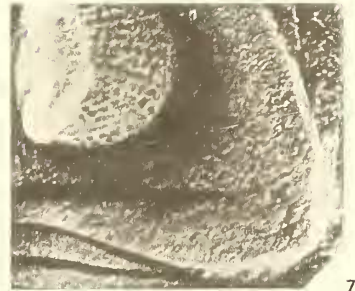
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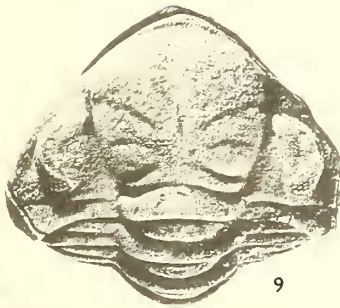
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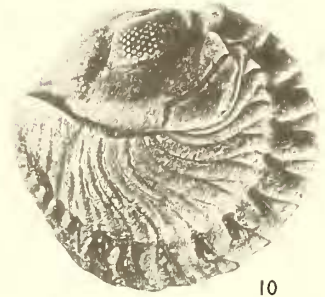
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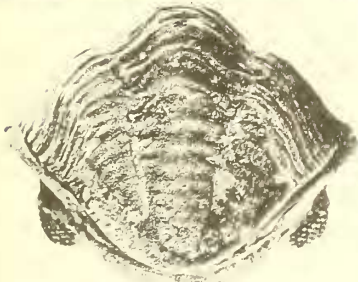
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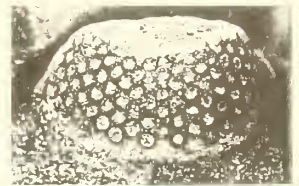
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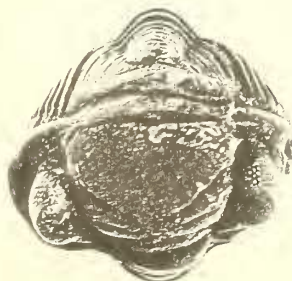
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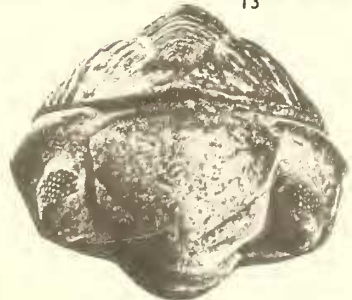
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the succeeding stages become gradually resorbed to give the angled adult condition (see below). Posterior border furrow transverse, deep but narrow (exsag.).

Eyes crescentic in plan, situated centrally between cephalic margin and glabella, on low ocular platform; extending from middle of 1L to anterior edge of 3L or to 3S; A/G, 46–67 per cent.; A/Gn, 37–54 per cent. Postocular area of fixigena relatively large, H/A 12–30 per cent. In lateral profile top of eye sloping gently to anterior; in anterior profile, well below surface of glabella. Palpebral lobes high; palpebral furrows generally well defined; palpebral areas relatively wide, with low inclination to axial furrows.

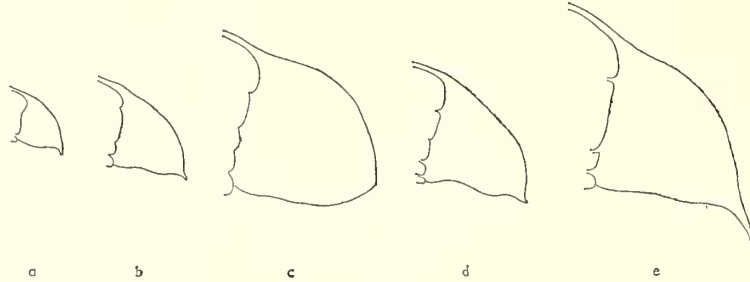
Visual surface overhanging slightly the ocular platform; gently convex or plane outwards; sloping more steeply outward-backwards than outward-forwards. Up to 168 lenses arranged in roughly alternating vertical columns containing at the maximum height of the surface 7 (8) or 8 (9) individual lenses, typically rounded or polygonal in outline and with a diameter of 0.2–0.255 mm. Interspaces granular, the granules arranged in a rough hexagonal network.

Hypostome subquadrate, anteriorly rounded, antero-laterally extended into short wings. Posterior margin straight, postero-lateral corners truncated. Lateral borders narrow, flat; posterior border more extensive. Median body adventrally convex, without distinct median furrow. Maculae forming small indistinct patches in anterior half of median body, close to lateral borders. Surface granulose.

Pygidium subtriangular in outline, margin entire at all growth stages; in posterior profile slightly vaulted; in lateral profile posterior margin curving gently addorsally. Axis raised above axial furrows and pleurae, moderately convex; composed of 8 axial segments in young, 8 (rarely 9) in adults, tapering to posterior and with a rounded, unsegmented terminal piece; segments 1–3 well defined, with strong transverse furrows; remaining segments becoming gradually less distinct to posterior. Pleurae moderately convex; 5 or 6 in young, 6 (rarely a trace of a seventh) in adults. Pleural furrows strong, interpleural furrows apart from the first, much weaker. Border wide at all growth stages. In young and juvenile forms the border is a smooth, unfurrowed extension of the pleural area but specimens with a pygidial length of 7.50 mm. and greater rapidly develop a flattening or shallow furrow at the junction of border and furrowed zones. Length: width of pygidium approximately $\frac{2}{3}$ – $\frac{3}{4}$.

Remarks. Although restricted to the variety α , *vulgaris* of Salter, there remains considerable variation within the species. This is mostly accounted for by changes taking place during the ontogeny. These changes may be summarized as follows. The glabella becomes apparently more parallel-sided; the frontal lobe slightly more convex; the furrows straighter; the strong posterior median deflections of the younger stages of both 3S and 2S gradually disappear; 1S becomes more transverse, less deep and less wide. In the pygidium 5 (6) pleurae are recognized in young holaspides; 6 (7) in large adults; a ninth axial segment may sometimes be discerned in large individuals. While in young and juvenile holaspide stages the border of the pygidium is merely an unfurrowed continuation of the pleural zone, the two become separated in adults with a cephalic length in excess of 7.50 mm. by a flattening or shallow furrow. Finally, and of importance phylogenetically, is the presence of short genal mucronations in very young holaspides with a cephalic length of up to 4.40 mm. Six specimens ranging in cephalic length between 2.72 and 4.40 mm. have been observed to possess these characters. The

mucronations are short and stout and are thrown off from the genal angle in a similar manner to the genal spines of *Acastella prima* Tomczykowa and *A. spinosa* (Salter) (text-fig. 3). They are not continuations of the cephalic outline as in the Dalmanitinae. Specimens with cephalic lengths within the range 4.50–7.50 mm. have very acutely angled genae with points in place of projections (text-fig. 3c), i.e. 'a tubercle only in



TEXT-FIG. 3. The development of the genal angle in *Acaste downingiae* (Murchison), compared to the genal condition of *Acastella prima* Tomczykowa and *Acastella spinosa* (Salter). a, Small holaspid of *Acaste downingiae* (cephalic length 3.2 mm.) showing genal projections; UN T5034. $\times 4$. b, Small holaspid of *A. downingiae* (cephalic length 4.3 mm.) SM A28744. $\times 4$. c, *A. downingiae*, juvenile holaspid, projection resorbed but genae remaining distinctly angled (cephalic length 8.8 mm.); NMW G.391.2. $\times 4$. d, *Acastella prima* Tomczykowa. Drawing after Tomczykowa 1962a (text-fig. 1c, p. 262). $\times 4$. e, *Acastella spinosa* (Salter), holotype, GSM 19412. $\times 4$.

place of a spine' (Salter 1864, p. 25). The specimen figured by R. and E. Richter (1954, pl. 3, fig. 39a) shows this stage in the development of its genal angles. Specimens with cephalic lengths greater than 7.50 mm. have less acutely angled genae, 'rounded off' (Salter, op. cit., p. 25), but still clearly show the positions from which the original projections were resorbed.

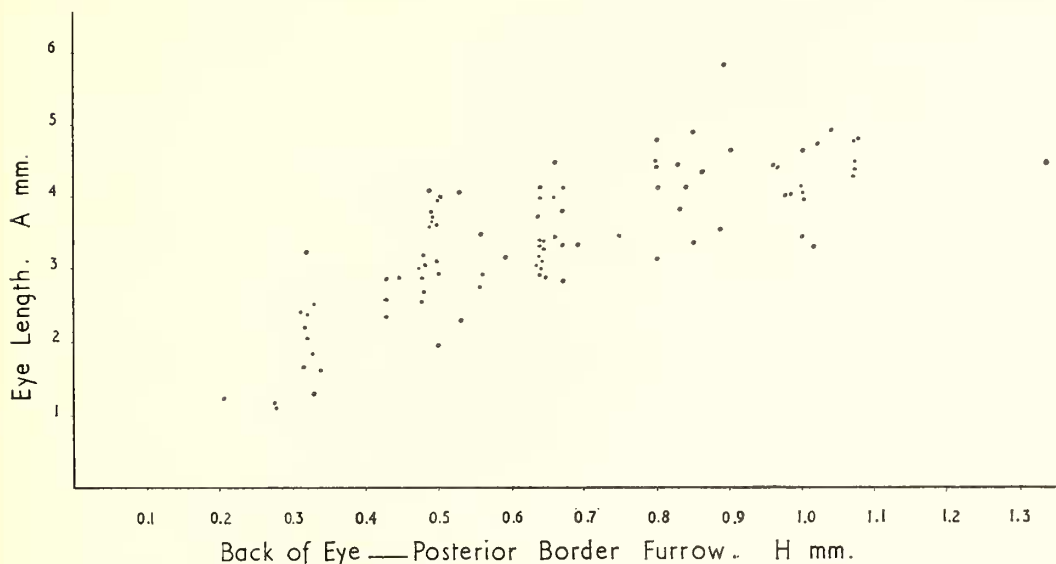
Apart from ontogenetic changes, further variation is observed in *Acaste downingiae*. Rarely, specimens are encountered in which 2S actually reaches and joins with the axial furrows in the adult stages. Equally rare are specimens in which not only 2S but also 1S fails abaxially to reach the axial furrow.

When values of A and H are plotted for 93 specimens of *A. downingiae*, the points are found to fall into five distinct groupings lying on a gentle curve (text-fig. 4). The possibility of a sixth is indicated by the solitary point at the extreme end of the graph. These groupings are interpreted as instars. Each group overlaps the preceding in values of eye length. Further, within each group, with the exception of the first, there appears to be a division into two fields, which is tentatively suggested as being the result of dimorphism.

Relationships. The relationships of *A. downingiae* (Murchison) to *A. inflata* (Salter) are dealt with under comments on the latter. R. and E. Richter (1954, p. 17) have made comparisons with their species, *A. dayiana*. The convexity and degree of tapering of the glabella and the number and distribution of the facets of the visual surface serve to differentiate the two species. No details of the ontogeny of *A. dayiana* are given. R. and E. Richter (1954, pl. 4, figs. 52–56) show, however, that when preserved with the shell,

the border of the pygidium and the furrowed pleural area are continuous, but in the internal mould a flattening separates the two areas.

As mentioned above, the adult of *Acastella prima* Tomczykowa possesses the mucronate projections characteristic of the smallest preserved holaspid stage of *A. downingiae* (text-fig. 3). The close relationships of the genus *Acastella* to members of the Acastinae



TEXT-FIG. 4. The eye length plotted against the distance of the eye from the posterior border furrow for 93 specimens of *Acaste downingiae* (Murchison). The graph shows groupings into five instars, with the possibility of a sixth.

are demonstrated further by Tomczykowa (1962*b*, p. 202) who derives *Scotiella* from it during the Upper Silurian, both genera occurring together in the Rzepin Beds (Upper Ludlow).

H. Hollard (1963, pp. 21–22, text-fig. 1*a–c*) has recently described, from the internal moulds of two pygidia, *Acaste talebensis*, a species of *Acaste* found near the junction of the *Monograptus uniformis* and *M. hercynicus* zones in Morocco. Both pleurae and axis of this species are more strongly convex (tr.) than the condition shown by *A. downingiae*. As a result the pleurae curve more sharply to the posterior. The interpleural furrows are more deeply incised than those shown on the internal moulds of *A. downingiae* and there are traces of segmentation, shown by slight swellings, on the border. The axial termination ends more abruptly and closer to the posterior margin. The two species share a similar outline and segmentation.

Range and Distribution. *Acaste downingiae* (Murchison) s.s. appears to be confined to the Wenlock Limestone of the Welsh Borderlands and West Midlands. Though it occurs typically in a calcareous environment, specimens similar to *A. downingiae*, from the Buckover Section, near Tortworth, Gloucestershire (Curtis and Cave 1964) occur in purplish-red and brownish weathering siltstones and yellow-brown fine-grained calcareous sandstone. Again, forms similar to *A. downingiae* occur in the grey-green calcareous siltstones of the highest Black Cock Beds (Lower Bringwood Beds) in the Golden

Grove, Llandeilo, and may even pass into the lowest Middle Bringewood Beds in the Llandovery area (J. F. Potter, personal communication). At Freshwater East, Pembs., *A. downingiae* is replaced by *A. subcaudata* (Murchison). The species has not been recorded from the Pen-y-lan inlier.

A. downingiae s.s. is definitely recorded from the following localities; Walsall, Staffs.; Dudley (Wren's Nest and Castle Hill), Worcs.; Benthall Edge, Salop; Wenlock Edge, Salop (rare); Malvern, Worcs.; Ledbury, Herefordshire.

Acaste inflata (Salter 1864)

Plate 29, figs. 9-16

1864 *Phacops (Acaste) Downingiae* Murchison, var. γ , *inflatus* Salter, p. 27, pl. 2, fig. 30 (OUM C9), not figs. 31 (GSM 19305), 32 (GSM 19314) or 33 (GSM 19306).

Lectotype (here designated). Salter 1864, pl. 2, fig. 30; OUM C9, figured here, pl. 29, figs. 9-14. Wenlock Limestone, Ledbury Railway Tunnel, Ledbury, Herefordshire.

Diagnosis. A species of *Acaste* characterized by its strongly convex (sag.) frontal lobe and by the high convexity (tr.) of 1L which causes it to slope abaxially well below the level of 2L; 2L and 3L are also more convex (tr. and sag.) than in *A. downingiae*, the convexity of the lobes causing the furrows to appear more closely spaced than in that species. Visual surface at maximum height with rows of 7 lenses alternating with 6. Pygidium with 7-8 axial segments, 5 pleural segments.

Description. Cephalon subtriangular in outline. Narrow, triangular area of librigena prominently projecting in front of glabella. Surface of test finely granular. Length of cephalon approximately $\frac{1}{2}$ - $\frac{2}{3}$ width.

Glabellar plan as in *A. downingiae*. Axial furrows gently curving round 2L and 3L. Frontal lobe rounded both anteriorly and antero-laterally, moderately to strongly convex (tr. and sag.). 2L and 3L abaxially fused, roughly equal in size, with slightly less convexity (tr.) than frontal lobe. 1L about half as wide (exsag.) as 2L, with much stronger convexity (tr.) than 2L in posterior profile, sloping abaxially well below the dorsal level of 2L. Side furrows 3S long, shallow, fairly wide, curving backwards with posterior median deflection. 2S shorter than 3S, impressed to similar depth, transverse, abaxially linear, medianly with marked deflection to posterior; failing laterally to join with axial furrows. 1S of similar length to 2S, wider and deeper, deflected both abaxially and medianly to anterior. Short sagittal furrow between median extremities of 3S. Side furrows appear closer together than in *A. downingiae* due to the greater convexity of the lobes (the 'crowded' condition of Salter 1864, p. 27).

Occipital furrow abaxially a little deeper than 1S, becoming shallow but still well defined sagittally. Occipital ring narrow (sag.), as wide (tr.) as 1L and with similar convexity (tr.); in lateral profile raised higher above the side lobes than in *A. downingiae*.

Genae strongly sloping to narrow flattened border. Preglabellar furrow shallow, very narrow (sag.). Postocular section of facial suture cutting lateral cephalic margin opposite middle of 2L; preocular section dorsal intramarginal, becoming marginal at antero-lateral edges of frontal lobe. Fixigenae postero-laterally angled in adults; with deep but narrow (exsag.) posterior border furrow.

Eye crescentic in plan, rather small; situated centrally between cephalic margin and

glabella, on high ocular platform which falls steeply to antero-lateral and lateral margins of cephalon. In lateral profile top of eye sloping gently to anterior; in anterior profile, well below level of glabellar surface. Eye extending from posterior margin of 1L to anterior margin of 3L; closer to posterior border furrow than in *A. downingiae*; H/A, 5–18 per cent.; A/G, 47–56 per cent.; A/Gn, 40–48 per cent. Palpebral lobes high; palpebral areas relatively wide, with low inclination to axial furrows.

Visual surface overhanging ocular platform; gently convex outwards. Up to 130 closely packed lenses arranged in roughly alternating vertical columns containing at maximum height 6 or 7 individual lenses, with a typical diameter of up to 0.2 mm. and rounded or polygonal in outline. Interspaces with similar texture to surrounding genae.

Pygidium subtriangular in outline, margin entire; in posterior profile slightly vaulted. Axis raised above axial furrows and pleurae; moderately to strongly convex; composed of 7–8 segments and a rounded, unsegmented terminal piece, tapering gradually to posterior; segments 1–3 well defined. Pleurae moderately convex; 5 in number. Pleural furrows strongly impressed, interpleural furrows weak. Border wide, as in adult *A. downingiae*, with a pronounced flattening separating the segmented and unsegmented pleural areas. Length of pygidium $\frac{2}{3}$ – $\frac{4}{5}$ width.

Comments on figured material. All the specimens used by Salter were derived from the Malvern–Ledbury area. His fig. 30 was obtained by Dr. R. B. Grindrod from the Ledbury railway tunnel. Figs. 31 and 32 were merely stated in 1864 to be from Ledbury, no stratigraphic horizon being given. In 1853, however, Salter (p. 9) recorded the same specimens from ‘the Wenlock limestones of the Malverns’ and from ‘the Wenlock Limestone, Ledbury’ respectively. Fig. 33 is said to be from Eastnor, near Ledbury.

In the text (1864, p. 27), it is implied that only fig. 30 represents the variety with any certainty. The diagnosis is given from this specimen as follows: ‘The glabella is greatly swollen, so as to be very convex, instead of flattened, in front. All the furrows are indeed distinct and in their proper situations, but from the inflation of the glabella they appear crowded. The eyes are small.’ Accordingly this specimen is here selected as lectotype for the species.

Of the other specimens figured Salter appears to have been less certain. Fig. 31, he states, ‘probably . . . belongs to var. β ’. This specimen has a similar furrow pattern to *A. inflata* but differs from it in the rather depressed frontal lobe more typical of *A. downingiae*: the low convexity of the glabellar lobes; the width (trans.) and convexity of the occipital ring and its failure to rise, in lateral profile, significantly above the glabellar side lobes. As such its characteristics are more compatible with *A. downingiae*, with which it is here included.

Fig. 32 is a cephalon of exceptional size (occipital glabellar length 20 mm., cephalic width 32 mm.). The eyes are missing. Although the frontal lobe is strongly convex (sag.), the side lobes lack the convexity typical of *A. inflata*. Furthermore, side furrows 3S and 2S are relatively shorter and the transverse convexity of 1L and the occipital ring are not nearly so pronounced as in that species. No other specimens referable to *A. inflata* approach anywhere near this specimen in size. Large specimens of *A. downingiae* have, however, been observed from the Ledbury area and of *Acastocephala macrops* from Pen-y-lan quarry, Cardiff. Due to its highly convex frontal lobe and deep side furrows this specimen has been refigured here with the latter species.

Fig. 33, a large pygidium (length 11 mm., width 15 mm.), is here certainly referred to the *downingiae* group. It has in common with that species 8 axial segments, 5 pleural segments, and the typical convexity when viewed in posterior profile. It is also wider than the typical pygidium of *A. inflata*.

Relationships. *A. inflata* appears to be closely related to *A. dayiana* R. and E. Richter from the Köbbinghauser Dayia-Schichten (see R. and E. Richter 1954, pp. 14–16, pl. 4, figs. 45–56). The frontal lobe of their species has a slightly greater convexity (sag.), and there is a higher degree of tapering of the glabella. The general glabellar plan and convexity of the lobes is very similar. At its maximum height the visual surface of *A. dayiana* carries rows of 5 lenses alternating with 6, and the total number of lenses borne by the surface is only 94. Although the two species have essentially similar cephalic outlines, the pygidium of *A. dayiana* is more subsemicircular than subtriangular in outline and is also apparently wider.

A. inflata is well differentiated from *A. downingiae* (Murchison) by virtue of its highly convex glabellar lobation. The visual surface of *inflata* carries 6 lenses alternating with 7, while that of *downingiae* has 8 alternating with 9. The eye of *inflata* is also a little closer to the posterior border furrow, H/A, 5–18 per cent. compared with 12–30 per cent. for *downingiae* (see text-fig. 2). Both cephalon and pygidium of *inflata* are slightly narrower than those of *downingiae*, the ranges of length/width for the cephalon being 51–68 per cent. and 46–62 per cent. respectively and for the pygidia, 65–85 per cent. and 60–80 per cent. In general it may be said that the pygidia are too closely related to be differentiated further. Compared with *downingiae*, the sample of *inflata* studied is small and the detailed ontogenetic changes have not been set out as for the former as the smallest holaspid stages have not yet been seen.

Range and Distribution. From the available material *Acaste inflata* appears to be confined, like *Acaste downingiae*, to the Wenlock Limestone of the Welsh Borderlands and West Midlands. Specimens close to *A. inflata*, however, occur in the siltstones and calcareous sandstones of the Buckover Section, near Tortworth, Gloucestershire (Curtis and Cave 1964). A further similar species with strongly convex glabellar lobes has been collected by the author from Lower Elton Beds outcropping near Upper Millichope, Shropshire.

The species has been identified with certainty from the following localities: Dudley (Wren's Nest), Worcs.; Malvern (railway tunnel), Worcs.; Ledbury (railway tunnel), Herefordshire.

Additional Material. *A. inflata* is not a common trilobite. The writer has seen to date but 19 specimens, the bulk of which are to be found in the Grindrod Collection, Oxford University Museum.

From the Wenlock Limestone of Ledbury; OUM C 559; specimens undocumented but probably also from this locality and horizon; OUM C597, C610, C612–20. From the Wenlock Limestone, Malvern; GSM 19301–3. From the Wenlock Limestone of Dudley; BM In36154, In36156; NMW 27.110.G.998.3.

Acaste subcaudata (Murchison 1839)

Plate 30, figs. 1–16

1839 *Asaphus subcaudatus* (n.s.) Murchison, p. 655, pl. 7, fig. 10.

1839 *Asaphus Cawdori* (n.s.) Murchison, p. 655, pl. 7, fig. 9.

1848 *Phacops Downingiae* Murchison; Salter, p. 336, pl. 5, figs. 2 (untraced), 3 (GSM 19377) and 4 (untraced).

1853 *Phacops Downingiae* Murchison; Salter, p. 1 (both *Asaphus Cawdori* and *A. subcaudatus* classed as junior synonyms of *P. Downingiae*).

1921 *Phacops Downingiae* (Murchison); Dixon, p. 21, footnote 6.

Holotype. Murchison 1839, pl. 7, fig. 10; GSC 6591. The holotype is 'possibly from the Wenlock Series' (Dixon 1921, p. 21), Freshwater East, Pembrokeshire.

Diagnosis. A species of *Acaste* with frontal lobe more strongly convex (sag.) than that of *A. downingiae* but less so than *A. inflata*; 3S more faintly impressed than in *A. downingiae*. Fixigenae of young holaspides with postero-lateral projections, resorbed in later moults, as in *A. downingiae*. Eyes small; visual surface narrow, similar to *A. dayiana*, with fewer lenses than *A. downingiae*, bearing at the maximum height rows of 5 lenses alternating with 6. Pygidium rather long; 7 (8) axial segments; 5 (6) pleurae; more strongly convex (tr.) than *A. downingiae*; border narrow, separated by marked flattening from furrowed pleural area at all holaspide stages. Margin entire throughout holaspide ontogeny.

Description (based on internal moulds). Cephalic outline subtriangular to ogival as in *A. downingiae*. The narrow, triangular area of librigena anterior to the frontal lobe which is common to other species of *Acaste* is also present in *A. subcaudata*.

Glabella anteriorly rounded, laterally more or less subparallel-sided, transverse width decreasing evenly to posterior. Axial furrows linear, without the gentle curve round 2L and 3L which characterizes *A. downingiae*, diverging at a slightly greater rate than *A. downingiae* in small specimens, appreciably less in large individuals. Frontal lobe anteriorly rounded, antero-laterally more parallel-sided than in *A. downingiae*. In lateral profile frontal lobe has a moderate convexity (sag.) which is greater than that of *A. downingiae* but less than *A. inflata*. Small individuals have a sagittal convexity similar to or greater than the adult of *A. downingiae*. 2L and 3L of roughly equal size, abaxially fused. 1L about half as wide as 2L; in young holaspides transverse convexity of 1L is slightly greater than that of 2L but in adults is less apparently so. 3S sigmoidal, long, more faintly impressed on the internal mould than in specimens of *A. downingiae* preserved with the shell, with a distinct median deflection to the posterior which appears to be present at all holaspide ontogenetic stages. 2S shorter than 3S, impressed to a similar depth, linear, transverse or with very faint posterior median deflection in some individuals; failing laterally to reach the axial furrows. 1S much wider and deeper but also shorter than 2S or 3S, curving both medianly and abaxially to the anterior.

Occipital furrow as wide and deep abaxially as 1S. Occipital ring narrow (sag.), with similar transverse width and convexity to 1L; in lateral profile barely rising above the level of the glabellar side lobes.

Fixigenae in young holaspides produced postero-laterally into short, stout projections which appear to be longer than in specimens of *A. downingiae* of corresponding size. In larger specimens the projection is resorbed but there remains a distinct point. Genal projections have been observed in specimens with a cephalic length of up to 2.9 mm. but a full range of sizes has yet to be collected. Adult genae are completely unknown, but those of intermediate stages are distinctly angled.

Eyes rather small, similar in plan to those of *A. inflata*, situated centrally on the genae on low ocular platform, as in *A. downingiae*; extending roughly from 1S to confluence of 3S and axial furrows; A/G, 45–63 per cent.; A/Gn, 37–46 per cent. In lateral profile the top of the eye slopes gently to the anterior and fails to reach the level of the glabella surface. Palpebral areas with low inclination to axial furrows. Fixigenal area between

back of eye and posterior border furrow similar in extent to *A. downingiae*, H/A, 12–27 per cent.

Visual surface known only from one juvenile specimen; rather narrow bearing fewer lenses than in *A. downingiae*, at the maximum height of the surface arranged in alternating columns of 5 or 6 (as in *A. dayiana*).

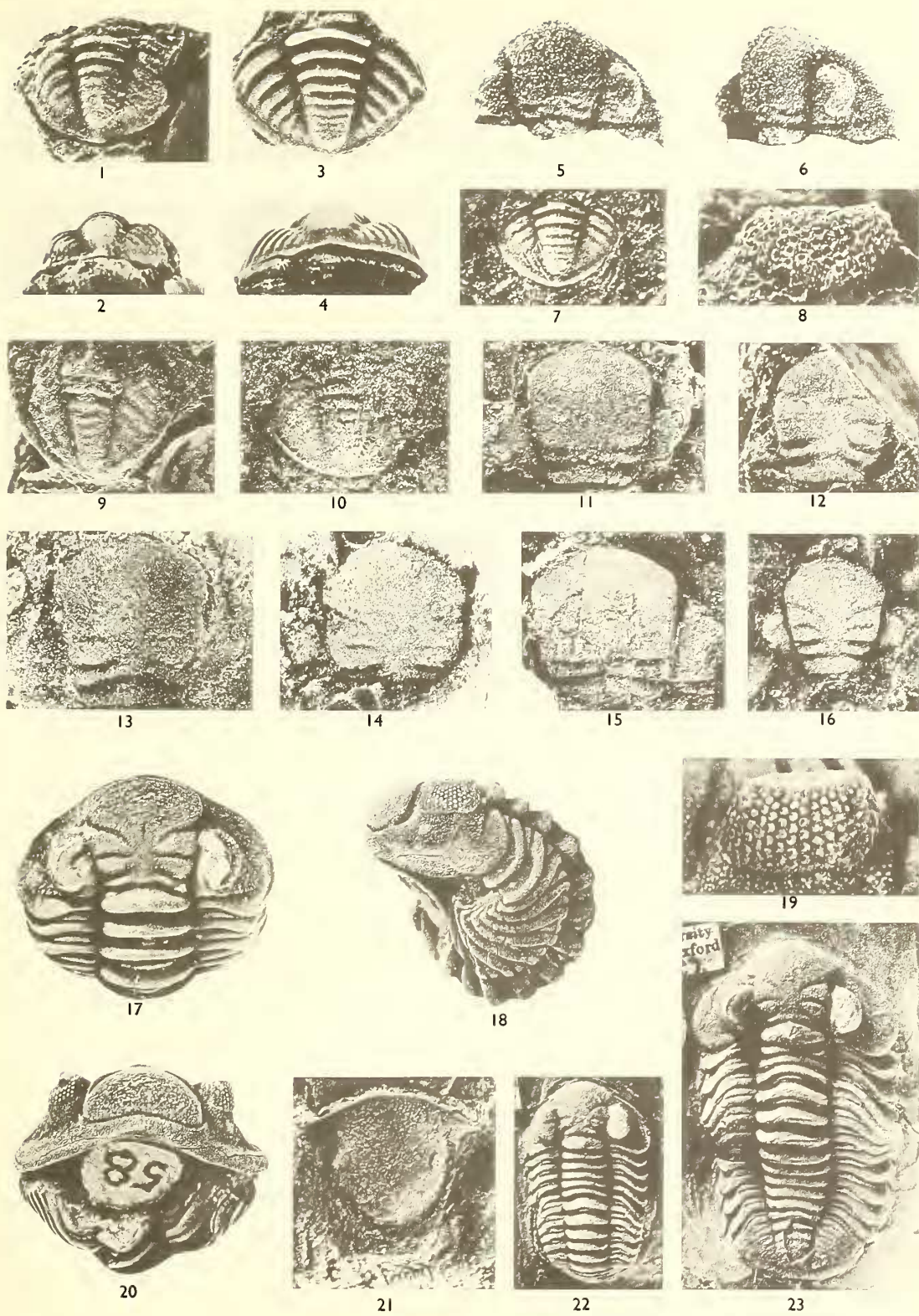
Outline of hypostome subrectangular; anterior margin rounded and antero-laterally produced into short wings; lateral margins very gently curved abaxially; posterior margin gently curved backwards; postero-lateral corners truncate, curved. Posterior border narrow, separated from median body by wide, well-defined furrow; lateral borders extremely narrow. Median body moderately convex adventrally. Maculae situated halfway along body, close to lateral borders.

Pygidium subtriangular in outline; in posterior profile rather strongly convex (tr.). Axis strongly convex (tr.), raised well above axial furrows and pleurae; typically with 7 (8) segments, the eighth being discernible only in cases of exceptional preservation; narrow postaxial border; axial segments 1–3 are most distinct, separated by well-defined transverse furrows; succeeding segments rather poorly defined towards the posterior. Pleurae generally more strongly convex (tr.) than in *A. downingiae*, falling off rapidly in postero-lateral direction; 5 (6) in number. Pleural furrows strongly defined, wide and deep; interpleural furrows, with the exception of the first, rarely preserved on internal moulds. Border narrow, separated from furrowed pleural area by a marked flattening at all holaspid growth stages. Margin entire throughout holaspid ontogeny.

Type Material. Specimens, GSC 6591 and 6592 are labelled as having been used by Murchison (1839) for his illustrations of *Asaphus subcaudatus* and *A. cawdori*. GSC 6591 is here selected as the holotype

EXPLANATION OF PLATE 30

- Figs. 1–16. *Acaste subcaudata* (Murchison 1839). 1–2. GSC 6591; Holotype; figured Murchison 1839, pl. 7, fig. 10. Probably Wenlock Series, Freshwater East, Pembrokeshire. 1, Dorsal view, internal mould of pygidium, $\times 3$. 2, View from posterior, $\times 3$. 3–4. GSM 19377; figured Salter 1848, pl. 5, fig. 3. Probably Ludlow Series, Freshwater East, Pembrokeshire. 3, Dorsal view, internal mould of pygidium, $\times 3$. 4, View from posterior, $\times 3$. 5–6. GSM 102597; Ludlow Series, Freshwater East, Pembrokeshire. 5, Internal mould of young holaspid cephalon with genal projection, $\times 4$. 6, Oblique view, $\times 4$. 7. GSM 102605; Ludlow Series, Freshwater East, Pembrokeshire. Internal mould of pygidium, $\times 3$. 8. GSM 102604; Ludlow Series, Freshwater East, Pembrokeshire. Internal mould of eye, $\times 8$. 9. GSC 6592; figured Murchison 1839, pl. 7, fig. 9 as *Asaphus cawdori*. Probably Wenlock Series, Freshwater East, Pembrokeshire. Internal mould of pygidium, $\times 3$. 10. GSM 102603; Ludlow Series, Freshwater East, Pembrokeshire. Latex cast from internal mould of pygidium, $\times 3$. 11. GSM 102602; Ludlow Series, Freshwater East, Pembrokeshire. Internal mould of cranium, $\times 3$. 12. GSM 102606; Ludlow Series, Freshwater East, Pembrokeshire. Internal mould of glabella, $\times 3$. 13–14. GSM 102600–1; Ludlow Series, Freshwater East, Pembrokeshire. 13, Internal mould of cranium, $\times 3$. 14, Latex cast from external mould showing side furrows 2S and 3S more deeply incised, $\times 3$. 15. GSM 102599, Ludlow Series, Freshwater East, Pembrokeshire. Internal mould of cranium, $\times 3$. 16. GSM 102598; Ludlow Series, Freshwater East, Pembrokeshire. Latex cast from external mould of cranium, $\times 3$.
- Figs. 17–23. *Acastoides constricta* (Salter 1864). 17–20. BU 58; figured Salter 1864, pl. 2, fig. 15a–c. Wenlock Limestone, Dudley, Worcs. 17, Dorsal view of cephalon, $\times 3$. 18, Lateral view, $\times 3$. 19, Eye, $\times 8$. 20, View from anterior, $\times 3$. 21. BM 58897; Wenlock Limestone, Dudley, Worcs. Hypostome, $\times 6$. 22. OUM C8; figured Salter 1864, pl. 2, fig. 14. Wenlock Shale, Malvern Tunnel, Worcs. Dorsal view, $\times 2$. 23. OUM C7; Lectotype; figured Salter 1864, pl. 2, fig. 13, 13a. Wenlock Shale, Malvern Tunnel, Malvern, Worcs. Dorsal view, $\times 2$.



for *Acaste subcaudata* (Murchison). In its segmentation, its degree of convexity and in the nature of its border, it is indistinguishable from the specimen (GSM 19377) figured by Salter (1848, pl. 5, fig. 3) and from others collected by the author from Freshwater East. GSC 6592, the holotype of *Asaphus cawdori*, is a specimen most difficult to evaluate, largely due to its distortion and indifferent preservation. There is also difficulty in equating it with Murchison's figures. Murchison (1839, pl. 7, fig. 9) originally figured a block showing two small pygidia but in 1872 (pl. 18, fig. 3) only one pygidium is depicted. In both illustrations the specimens are complete and undistorted. GSC 6592, therefore, can only doubtfully be identified with *A. cawdori*. Essentially similar to *Acaste subcaudata* in construction it is here included with reserve in the synonymy of that species. Stubblefield (1938, p. 31) states that Salter's fig. 2 (pl. 5) has been possibly compounded from two specimens in the Geological Survey Collections, GSM 19376 and 19378, both being incomplete cranidia and neither showing the full outline or extent of the cephalon as depicted by Salter. The specimen used for fig. 3 is thought to be GSM 19377. That used for fig. 4 is untraced.

Relationships. *A. subcaudata* differs from *A. downingiae*, to which it is closely related, by its more convex (sag.) frontal lobe; by the tapering of the glabella; the depth of impression of the side furrows, which would normally be expected to be deeper on the internal mould (the furrows must be quite faint on the shell); the number of facets of the eye and their distribution; the general shape of the hypostome and the convexity and segmentation of the pygidium.

From *A. inflata*, *A. subcaudata* differs by the lower convexity (sag.) of the frontal lobe; the lower convexity (tr.) of the preoccipital glabellar lobe; by the number and distribution of eye facets and by the same pygidial characters as stated above for *A. downingiae*.

A. dayiana has a more strongly convex (sag.) frontal lobe and a greater degree of glabellar tapering. The convexity (tr.) of the side lobes would also appear to be stronger. Pygidial segmentation and the presence of a border flattening on the internal moulds are common to both species, as is the content of the visual surface. A common environmental control may account for these similarities.

Range and Distribution. *A. subcaudata* is at present only known from strata occurring at Freshwater East, Pembrokeshire, attributed by Dixon (1921) to the Wenlock and Ludlow Series. GSM 102597-606 were collected by the author from the Ludlow Series of the South side of Freshwater East Bay, from rottenstone bands in group (4) of Dixon (1921, p. 14). These beds are accessible where the High Water Mark shown on Dixon's sketch map (1921, p. 23) is marked as meeting the cliff. Approximate Grid Ref., SS 0168/9739.

Additional Material: GSM 19376-8, 102597-606.

Genus *ACASTOIDES* Delo 1935
Acastoides constricta (Salter 1864)

Plate 30, figs. 17-23

- 1864 *Phacops (Acaste) Downingiae* Murchison, variety or subspecies ϵ , *constrictus*. *Phacops constrictus*. Salter, pp. 27-28, pl. 2, figs. 13 (OUM C7), 14 (OUM C8), 15 (BU 58).
1954 *Acaste (Acastoides) constricta* (Salter 1864). R. and E. Richter, pp. 17-18, pl. 3, figs. 42, 43.
1965 *Acastoides constricta* (Salter 1864); Clarkson, p. 22, pl. 3, figs. 10-12.

Lectotype (here designated). Salter 1864, pl. 2, fig. 13; OUM C7. Wenlock Shale, Malvern Tunnel Malvern, Worcs.

Remarks. R. and E. Richter (1954, pp. 17–18) have given an account of this species but have omitted to consider the hypostome. Accordingly no detailed description will be given here. Instead, an extended diagnosis is given together with an account of the hypostome and notes on the relationship of *Acastoides constricta* with other species of the genus.

Extended diagnosis. A species of *Acastoides* characterized by a strongly convex (sag.) frontal lobe which frequently extends to the anterior margin of the cephalon; 1L with a greater transverse convexity than 2L, sloping abaxially below the level of 2L; 3S shallow, wide, sigmoidal, with strong posterior median deflection; 2S long, transverse, just reaching the axial furrow; 1S and 3S tending to converge adaxially. Occipital ring raised high above level of glabella, with axial node. Genae postero-laterally rounded off. Preocular section of facial suture marginal or just dorsal intramarginal. Eyes small, close to glabella, extending from occipital furrow to anterior edge of 3L, raised on high ocular platform nearly to the level of the glabella. Palpebral lobes high; palpebral areas narrow, with high inclination to the axial furrows. Visual surface with 104+ lenses, at maximum height bearing columns of 6 alternating with 7. Pygidium subsemicircular in outline, posteriorly truncate, scarcely vaulted in posterior profile; margin entire. Axis short, with low convexity (trans.), composed of 5 (6) segments and wide axial terminal piece. Pleurae weakly convex (trans.), 4 in number; furrows weakly impressed, pleural furrows being slightly stronger than interpleural furrows. Border flat and broad.

Hypostome outline subquadrate; anterior margin arcuate, antero-laterally extended into short wings; lateral margins curving very gently abaxially; posterior margin short, gently curved backwards; postero-lateral margins truncate. Lateral borders narrow; posterior border wide (sag.). Median body strongly convex adventrally, without trace of median furrow. Maculae large, ovoid and prominent, situated on lateral margins of median body just inside the anterior half of the structure. Surface coarsely granular.

The hypostome of *A. constricta* (Salter) differs from that of *Acaste downingiae* in its more highly convex median body with prominent maculae; in the arcuate outline of the anterior margin and the wide (sag.) posterior border. Though similar in structure to the hypostome of *Acastocephala macrops* (Salter), that of *Acastoides constricta* contrasts strongly by its distinctive coarse ornament.

Relationships. In construction the cephalon of *Acastoides constricta* appears to be closely related to *A. heuni heuni* R. and E. Richter 1952 described from the Wiltzer Schichten, Upper Emsian. *A. constricta* may be differentiated by its more marginal frontal lobe; greater degree of glabellar tapering; eyes larger and more extensive; visual surface with a greater number of lenses and a maximum of 7 in any column compared with 4 in *A. heuni heuni*; the pygidial margin is entire and non-denticulate.

A. constricta is similarly distinct from *A. heuni posthuma* R. and E. Richter 1952 from the Heisdorfer Schichten, high Upper Emsian, and from *A. paeckehuanni* R. and E. Richter 1939, from the Pendik Schichten, Pendik, Bosphorus, high Upper Emsian in age.

Range and Distribution. *Acastoides constricta* is recorded from the Wenlock Shale and Wenlock Limestone of Dudley, Walsall and the Malvern Tunnel, Malvern, Worcs. It appears to be restricted to the Wenlockian of the Welsh Borderlands.

Additional Material. In addition to the lectotype and paratypes the following material has been located.

From the Wenlock Shale of the Malvern Railway Tunnel: OUM C561-7, C576, C609, C611; BM 59040, 59048; GSM 19242-3. From the Wenlock Limestone, Malvern; BM 44251; GSM 19304; labelled Wenlock? Limestone, Malvern; BM 58897, 59048; labelled simply Malvern; GSM 49836. From the Wenlock Limestone, Walsall; GSM 22450. Unlocalized specimen; GSM 49838.

Family DALMANITIDAE Vogdes 1890

Subfamily ACASTAVINAE Struve 1958

ACASTOCEPHALA gen. nov.

Derivation of name. Trilobites with cephalon constructed in a similar manner to that of *Acaste* Goldfuss.

Type species. *Acastocephala macrops* (Salter 1864).

Other species. *Acastocephala dudleyensis* sp. nov.

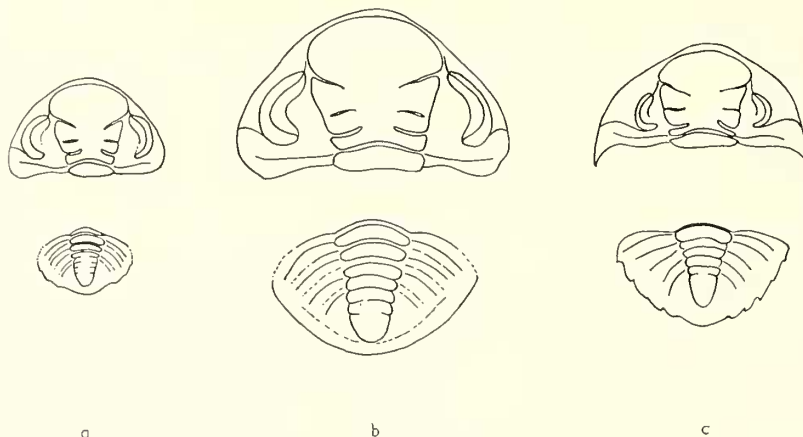
Diagnosis. Cephalon typically acastid in construction but with larger eye; visual surface containing, at maximum height, rows of 10 lenses in *A. macrops* (Salter), 9 in *A. dudleyensis* sp. nov. Pygidium wide, weakly furrowed; 4-5 pleural segments; 7 axial segments. During ontogeny of both known species smallest holaspides have a denticulate lateral pygidial margin; denticulations resorbed in succeeding growth stages to give adult with typically entire margin.

Range and Distribution. Wenlock Shale, Malvern, Worcs; ? Wenlock Shale, Pen-y-lan, near Cardiff; Wenlock Limestone, Malvern and Dudley, Worcs.

Relationships. *Acastocephala* differs from *Acaste* Goldfuss in the following characteristics. The eye is larger, carries a greater number of facets and is relatively closer to the posterior border furrow. The pygidium has a lower convexity (tr.) and is more poorly segmented. Both pleural and interpleural furrows are weaker. As in *Acaste*, the fixigenae of the smallest holaspides are provided postero-laterally with short projections but these are not nearly so long or distinct and appear to be more rapidly resorbed. In addition, young holaspides of *Acastocephala* have a denticulate lateral pygidial margin which contrasts with the entire margin of the adults, while the margin of *Acaste* is entire in holaspides of all sizes. Posteriorly the margin is without trace of a caudal projection. The hypostome is larger and more convex (tr. and sag.) than in *Acaste* and the maculae are larger and more clearly defined.

Though closely related to *Acaste*, *Acastocephala* is equally close to *Acastava* R. and E. Richter 1954. The glabella are essentially similar in construction. Schmidt's text-figure of *Acastava atava* (1907, p. 10) shows side furrows 3S to be obliquely directed, without a posterior median deflection and very similar to the condition of *Acastocephala macrops*. Similarly, 2S is linear, transverse and only just failing abaxially to reach the axial furrows. In *Acastava atava* the eyes are large but the visual surface at its maximum height contains columns with only 6 lenses. *A. atava* also differs in retaining genal spines into adult holaspide stages. When preserved with the shell the pygidial margin of *A. atava* is entire but the internal mould possesses 5 pairs of lateral denticulations (see Schmidt 1907, p. 10, text-fig. 1 and R. and E. Richter 1954, pl. 6, figs. 81 and 82) formed in exactly the same manner as those produced in young holaspides of *Acastocephala* (text-fig. 5). Pygidial

segmentation is also similar. *Acastava? schmidti* (R. Richter), like *Acastocephala dudleyensis*, possesses large eyes situated both close to the glabella and to the posterior border furrow. *Acastocephala* is confined, in the British Isles, to the Wenlockian while *Acastava* ranges in the Lower Devonian from Siegenian to Emsian. The affinities between these two genera may prove to be significant phylogenetically.



TEXT-FIG. 5. A comparison of *Acastocephala macrops* (Salter) and *Acastava atava* (W. E. Schmidt). *a*, Young holaspid of *A. macrops* showing lateral denticulations on pygidial margin of shell; BU 862. $\times 2\frac{2}{3}$. *b*, Adult of *A. macrops* showing entire pygidial margin; BU 861. $\times 2$. *c*, Adult of *Acastava atava* showing denticulations along lateral pygidial margin on the internal mould. Drawing after Struve 1959, p. O476, fig. 377, 1a, 1b. $\times 2\frac{2}{3}$.

Acastocephala is quite distinct from *Acastella* Reed 1925. *Acastella* is characterized by slender genal spines and by a caudal mucronation throughout its ontogeny. Pygidial segmentation and the size and position of the eyes in *Acastella* are essentially similar to *Acaste*. Some species of *Acastella* have a smooth pygidial margin when preserved with the shell or as internal moulds as, for example, in *A. heberti heberti* (Gossellet), *A. patula* Hollard, and *A. jacquemonti* Hollard. Others, *A. tiro* R. and E. Richter and *A. heberti elsana* R. and E. Richter, produce lateral denticulations on the internal mould but not on the shell.

The genus *Acastoides* Delo 1935, is characterized by a subpentangular cephalic outline and eyes set high up on the genae. The shape, convexity and segmentation of the pygidium differ considerably from *Acastocephala*. In some species, *Acastoides henni henni* (R. Richter) and *A. paeckelmanni* R. and E. Richter, there is a tendency to develop spine-like denticulations along the pygidial margin but they differ from those of *Acastella*, *Acastava*, and *Acastocephala* in that they are directed ventrally. *Acastoides constricta* (Salter) and *Acastocephala macrops* (Salter) occur together in the Wenlock Shale of Malvern.

The decision to erect a new genus to cover trilobites referred to Salter's variety *macrops* is based largely on the differences of these species from both *Acaste* and *Acastava*. The larger number of eye facets and the lack of genal spines in the adult prevent inclusion of these trilobites in the genus *Acastava*, while the pygidial margins of the young and

weaker pygidial furrowing preclude their inclusion in the genus *Acaste*. A further consideration has been the possibility of a phylogenetic link between *Acastocephala* and *Acastava*.

Acastocephala macrops (Salter 1864)

Plate 31, figs. 1–15, Plate 32, figs. 1–2

1864 *Phacops (Acaste) Downingiae* Murchison, var. β , *macrops*, Salter, pp. 26–27, pl. 2, figs. 27 (BU 861), 29 (GSM 19319), 32 (GSM 19314), *not* figs. 26 and 28 (specimens untraced).

Lectotype (here designated). Salter, 1864, pl. 2, fig. 27; BU 861. Wenlock Shale, Malvern, Worcs.

Diagnosis. A species of *Acastocephala* gen. nov., with moderately convex (sag.) frontal lobe; 3S wide and deep, opening out abaxially, 2S short, linear, sloping gently abaxially to posterior. Eyes large, situated centrally on the genae; extending anteriorly past the confluence of 3S and the axial furrows. Visual surface at maximum height bearing 9 lenses alternating with 10. Pygidium with low convexity; 4 (5) pleurae, 7 axial segments. Border undifferentiated from furrowed pleural area. Margin in small holaspides denticulate, entire in adults.

Description. Cephalic outline ogival, subtriangular or in large individuals, more rarely, subsemicircular. In common with species of *Acaste* and *Acastella* there projects, anterior to the glabella, a narrow triangular area of librigena, in this species not as extensive as in *Acaste downingiae* or *Acaste inflata*. Surface of test finely granular. Length: width of cephalon $\frac{1}{2}$ – $\frac{2}{3}$.

Glabella anteriorly rounded, laterally subparallel. Angle of divergence of axial furrows similar to *A. downingiae*. Degree of tapering in transverse width rather irregular, giving, in some specimens, a distinctly waisted appearance (cf. the lectotype), which is less apparent in specimens which have either lost the greater part of their shell thickness or are preserved as internal moulds. Frontal lobe both anteriorly and antero-laterally rounded, with moderate to strong convexity (sag.) in young holaspides and adults. 2L and 3L laterally fused, more or less equal in size, slightly less convex (tr.) than the frontal lobe. 1L narrow (exsag.), about half the size of 2L. Convexity (tr.) of 1L insignificantly greater than 2L in specimens with shell but slightly greater in internal moulds. 3S long, sigmoidal, wide and deep, opening out and becoming deeper abaxially; with distinct posterior median deflection in the majority of specimens. 2S shorter, less deep than 3S, linear, transverse, sloping gently to the posterior abaxially, generally failing laterally to join with axial furrows but in some examples very nearly attaining this condition. 1S only a little deeper than 3S, longer than 2S, deflected both medianly and abaxially to anterior.

Occipital furrow impressed to similar depth as 1S. Occipital ring typically a little wider (trans.) than 1L and with similar convexity (tr.). In lateral profile failing to rise significantly above level of glabellar side lobes.

Genae restricted in area due to size and position of eyes. Postocular section of facial suture cutting lateral cephalic margin opposite the posterior edge of 2L; preocular section dorsal intramarginal but may become almost marginal at antero-lateral margins of glabella as in *Acaste inflata*. Genae postero-laterally angled in young holaspides, rounded in adults.